

NOTES ON THE LIFE-HISTORY OF SOME NORTH AMERICAN LAMPYRIDÆ.<sup>1</sup>

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## INTRODUCTION.

This paper represents the biological portion of two years' work at the Bussey Institution on several species of beetles of the subfamily Lampyrinæ or true fireflies. The portion dealing with the embryology, and the structure and development of the light-organs of two common species, *Photuris pennsylvanica* DeGeer and *Photinus consanguineus* Leconte, together with illustrations of these two fireflies and their early stages, has recently appeared in the Journal of Morphology. The observations on the life-histories were made throughout the year but especially during the summer both in the field and in the laboratory. For collecting Lampyrinæ and particularly their larvæ, a small electric flashlight was found to be indispensable.

I wish to thank all those who have helped me in my work and especially Dr. Wm. M. Wheeler for many helpful suggestions and criticisms.

## PREVIOUS BIOLOGICAL WORK ON FIREFLIES.

Comparatively little work has been done on the life-history and habits of American fireflies. In Europe, where more is known of the Lampyridæ than in our own country, *Lampyris noctiluca* L. has furnished more data than any other species. The male of *noctiluca* is fully winged but only faintly luminous, the female, on the other hand, is apterous and larviform and glows brightly. Newport, whose work was done from 1830 to about 1842, furnished a good general account of the life-history of this glow-worm. Olivier (1911, etc.), Fabre (1913), and others have also contributed biological data, but the most recent publication is that of Vogel (1915), who gives data on the larva of *Lampyris noctiluca* in relation to its life-history, and an excellently illustrated description of the external anatomy, as well as

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the structure of the mouthparts, pharynx, gizzard, etc. Especially valuable is the portion relating to the operation of the mouth-parts in connection with the poisonous secretion which is emitted through the mandibular canal.

Among those who have contributed to the life-history of North American Lampyridæ, Barber (1905 and 1914), Mast (1912), and McDermott (1910-1912) are deserving of special mention.

*Photinus consanguineus* Lec.<sup>1</sup>

This is a rather slender, quite depressed insect, with the head well retracted under the prothorax. The antennæ are eleven-jointed and moderately slender, and the eyes are larger in the male than in the female. The prothorax is rounded anteriorly and at the sides, and truncate behind, with the posterior angles rather acute, the disc is convex with the margins broad and thin. The elytra have rather narrow side margins and two or three subobsolete carinæ, the legs are rather short, with the femora and tibiæ rather compressed. The abdomen is depressed, and in the male, bears the light-organ on the sixth and seventh sternites, while in the female it occupies the greater part of the seventh sternite. The head is largely blackish, the thorax yellowish, with a broad black median bar on its posterior half and bordered on each side with pinkish. The elytra have the suture and side margins pale yellowish, the legs are brownish and the abdomen, except for the pale yellow luminous area and the pale segments beyond on the ventral side, is blackish. The elytra are granulate and rather densely pilose, while the antennæ and the legs have short, glossy brown pile. The beetle measures from 8 to 12.5 mm. in length.

During June and July, this firefly is very abundant about Boston, and in the evening may be seen flashing its yellowish light in the low moist meadows. The males are active though not rapid flyers, but the females, while provided with wings, are not taken in flight. It is evident that the light-organ (situated on the sixth and seventh sternites in the male and occupying the greater part of the seventh in the female) serves as a secondary sexual character, but it is difficult, if not impossible, to explain the purpose of the larval light-organ. The mating responses of fireflies have been studied by McDermott (1910-

<sup>1</sup> *Photinus consanguineus* Leconte; Proc. Phil. Acad. Nat. Sci., V, 335, 1851.

1912), and by Mast (1912), among others in this country. I can add but little to their observations. The males of *Photinus consanguineus* are on the wing shortly before 8.00 P. M., and a half hour later the flashing is at its height, while after 9.00 P. M., there is a decrease. The female crawls up some weed or grass stem and emits a single strong, diminishing flash in response to the three or four flashes at rather long intervals, of the male, which may be flying nearby or perched on an adjoining weed. I can do no better than to quote Mast (p. 267-268): "The luminous or photogenic tissue in the female as previously stated is confined to a small area on the ventral surface of the third segment from the end. Just before the female glows in response to the flash of light produced by a male she raises and twists the abdomen so as to direct the ventral surface, the source of light, toward the male. If the male is directly above she twists the abdomen nearly through 180 degrees, if to the right or left through 90 degrees, etc. Only when the male is directly below does the female glow without twisting the abdomen. These responses occur in the western Maryland species, almost invariably, and they are so striking that they cannot be readily overlooked." This species flashes but once in either sex. Further observations by McDermott show that different species of *Photinus* have a characteristic mode of flashing. In *Ph. consanguineus*, in the few instances under my observation, the male, in response to the female, would alight near the latter and search about excitedly, flashing in the meantime, and the female would respond in a rather feeble manner to the male, but a few inches away. Often considerable time elapsed before the male found his mate.

Neither sex was observed to eat anything, nor could the stomach contents of alcoholic specimens be determined. Bowles (1882), speaking of *Lampyris noctiluca*, a European genus allied to *Photinus*, says: "The perfect insect is herbivorous and feeds only on the tender leaves of plants; but the larva is voracious in its habits, devouring snails, slugs and soft-bodied insects."

*Ph. consanguineus* oviposited readily in captivity, but the number of eggs laid by a single specimen was not ascertained. The eggs are deposited among fine grass roots or a short distance in the soil. The egg measures about 0.750 by 0.666 mm. It is dull creamy white, and smooth under a hand lens. A thin membrane with oil-like dots envelops the chorion. The egg is at first quite soft and often consid-

erably flattened against the surface to which it adheres by the viscosity of the outer membrane. Newport ('57), speaking of *Lampyris noctiluca*, states that at the moment of laying, the egg is covered with a very adhesive sticky matter. Later the egg becomes firmer and loses much of this stickiness. The laboratory period of incubation was from about thirteen to fifteen days, a large batch of larvæ hatching about July 24 in 1913. According to Newport, the egg state of *Lampyris noctiluca* is about nineteen days. Vogel ('15) says that oviposition of the same species usually occupies two or three days and incubation twenty-seven to thirty, thirty-six, and even forty-seven days, according to the temperature of the summer. *Photinus* larvæ which are ready to emerge have conspicuously black eyes and brown mouth-parts.

When freshly hatched the larva is about 2.35 mm. long, and whitish, except for the blackish eyes and brown mouth-parts. Soon it becomes slaty gray with the head largely brownish. Its length, exclusive of the retractile head, a few days later is 2.5 mm., and the width at the second thoracic segment is 0.6 mm. The form is oblong-elongate, broadest at the thorax and thence tapering gradually toward the caudal extremity. The body is depressed, and rounded-carinate mesially. There is also a subdorsal carina on the thorax, which is less distinct on the abdomen and which marks the course of a pale stripe. The head is about half as wide as the prothorax and nearly or quite as long as the latter; the antennæ are three-jointed, the third joint is strongly chitinized and bears one globular and one cylindrical sense-organ distally. The mandibles are arcuate, with a finely pointed tip and a projecting præapical internal ridge. The legs are slender and spinose, and under high magnification the body appears roughly granulate. The single pair of prolegs is strongly multifurcate, and the many filaments are thickly armed with rows of ventral hooks, which occur also along the base of the furcation. The larva has well-developed light-organs in the form of two small lenticular structures in the ventral portion of the eighth abdominal segment. These glow with a yellowish light.

The duration of the first instar of *Lampyris noctiluca* is about fifteen days according to Newport ('57). The first moult occurs nineteen days after hatching. Under artificial conditions I found the young *Photinus* larvæ quite delicate, and I was able to carry but few

over into the third instar. When ready for the first moult they are about 3 mm. long. I kept these insects in a jar of moist earth and fed them flies which were cut up so that they could be devoured more easily. Several larvæ would gather about a fly and bore their way into it till their heads and a portion of the prothorax were hidden from view. They remained thus for some time, so that when a day later I examined the larvæ, I found them all dead from suffocation. Like *Photuris*, they pass the greater part of two years as larvæ, and like the former, the same brood is sometimes characterized by the unequal growth of some of its individuals, so that there are larvæ which probably require less and others more than two seasons to produce adults. No first-year larvæ were taken in the field. Newport, in rearing *Lampyrus noctiluca*, noticed different rates of growth among the larvæ under apparently the same conditions. He adds that they may not all mature the same year, for as much as one year and nine months may elapse before full growth is attained.

The full-grown larva is about 13 mm. long, exclusive of the head, and with the head extruded, 14.5 mm. The head is depressed, sub-cylindrical, somewhat longer than wide, and about half as wide as the prothorax. The antennæ are three-jointed, with two terminal sense-organs. The body is slender and depressed and a little wider at the middle. The tergites are heavily chitinized and coarsely punctate and rugose, while on each side of the dorsal median line is a rather indistinct carina, most evident on the thorax and tending to disappear posteriorly. The legs are slender and the prolegs very much divided into dichotomously branching filaments. The dorsum is shining black, the ventral sclerites are smoky brown and the membrane is dirty whitish, with the exception of the venter of the thorax as well as the sides above the lateral line, where there is often a decided suffusion of pinkish. The legs have the chitinous portion testaceous. The head is black and the mandibles reddish brown. The body has rather sparse yellowish-brown hair. The adipose tissue gives the anterior part of the body a pinkish tinge. The larvæ of *Ph. pyralis* (Rep. N. J. State Mus., p. 298, 1909) and *Ph. modestus* (Kellogg's American Insects, p. 269) much resemble that of *consanguineus*.

It seems evident that a larva of the form of *Photinus* is not so well fitted to lead an active life above ground as that of *Photuris*. As a matter of fact, it is much more subterranean in its habits and



therefore less frequently seen and taken. It also inhabits damper situations. Larvæ were found in the fall, winter and spring of the year, but most abundantly in the fall. Upwards of one hundred were secured, mostly from September 8 to October 5, 1913. On March 20, 1915, a few hibernating individuals were taken in a moist field, where they lay buried a few inches in the soil. They occurred in a small hummock which remained unfrozen. Active specimens were found on May 11, 1914. On warm summer nights as many as fifty could be taken in two hours. Some of these larvæ were a little off the ground, crawling along blades of grass, while others were creeping about the damp soil. They occurred most plentifully in the earth-choked channel of Bussey Brook at Forest Hills, Boston. In May, 1914, the low meadow, where I procured larvæ the preceding year, in many places stood an inch or more under water, which must have forced many of the insects out of the soil, for some were found a short way up stems while a small hummock yielded others.<sup>1</sup> The larvæ are more or less gregarious, at least during the later stages, for they gathered together in captivity, and were taken singly or more commonly in small groups under wood or other debris in their habitat, while another species of the same genus was found in some numbers under a sheltered piece of decayed wood. It would seem that their life is largely subterranean, and that they come to the surface only under more favorable conditions or during excessive moisture. In the laboratory large larvæ thrive with very little care in a jar of moist earth. At long intervals they were fed with earthworms which they paralyzed after the manner of *Photuris*. But they were by no means as voracious as the latter.

The pupal stage is quite brief. Pupating larvæ lose their bright

<sup>1</sup> In this connection it is interesting to note that Annandale, '00 and '04, twice found an aquatic lampyrid larva in lower Siam, and once in the suburbs of Calcutta. In the case of the Siamese specimens, the luminous organs were two small oval patches on the ventral surface of the last abdominal segment. As in other lampyrid larvæ the light shone steadily, though it was of a brilliant blue color. Many fireflies were flying over the marsh where Annandale took some of the larvæ. The latter he found clinging dorsal surface downwards to floating fronds of a small cryptogam. They ceased to shine on being taken out of the water, but the luminescence was resumed upon immersion in the liquid. No special respiratory organs nor air-silvered areas were found. He did not rear the larva to maturity.

color, shorten up a little and assume an arcuate position. The skin splits down the anterior part of the back and gradually liberates the pupa. The latter is formed under the soil.

The pupa, straightened out, measures about 11 mm., and in an arcuate position, 8 mm. It is depressed subcylindrical, with the appendages rather short and the lateral tergites only slightly drawn out and hardly reflexed. It bears, especially along the edges of the segments, some short and quite sparse hairs. The general color is yellowish white with a considerable suffusion of pinkish, especially along the abdomen. It is much less active than the pupa of *Photuris*, and, unlike the latter, never has a general effulgence. The larval light-organs shine steadily during the pupal life but are somewhat smaller and are rather more evident during the earlier than in the later pupæ, where the cuticula is much pigmented. By the time that the perfect insect is freed there is usually little or no luminescence in the larval organ.<sup>1</sup> Laboratory specimens which pupated during the winter were nearly all females.

#### *Photinus scintillans* Say.<sup>2</sup>

This species occurs more rarely in the neighborhood of Boston than *consanguineus*, and is found on drier, higher ground, often associated, though to its own detriment, with *Photuris pennsylvanica*. Besides differing from its congener in its smaller size and more slender legs, as well as paler color, the male may also be distinguished by the fact that it (as well as the female) emits but a single, rather long flash to the three or four flashes of the male *consanguineus*. The female seems incapable of flight, and specimens are often met with having the abdomen protruding far beyond the elytra. The semi-gregarious larvæ are paler and more suffused with pinkish than *consanguineus* larvæ. A few of the larvæ were found upon the surface of the ground, and several large ones, superficially buried in the light soil, were taken in the evening.

#### *Ellychnia corrusca* Linn.<sup>3</sup>

<sup>1</sup> In some cases at least, there is a rather brief period in the pupal stage during which neither the larval nor the adult photogenic organs glow. Such a case was observed on December 14, 1913. A pupa, apparently less than a day from hatching, could not by rough handling, jarring, etc., be induced to give any light whatsoever, though the adult organ was plainly visible.

<sup>2</sup> *Photinus scintillans* Say, Journ. Phil. Acad. Nat. Sci., V, p. 163, 1825.

<sup>3</sup> *Ellychnia corrusca* Linn., Syst. Nat., Ed. XII, 644, 1785.

This is a very common firefly, a rather broad flat species, with a small retractile head, slaty black elytra and a pinkish stripe on each side of the disk of the thorax. It belongs to the *Photinus* group, and like the members of that genus, is capable of giving forth a viscous milky exudation and of clinging tenaciously to one's fingers. But it differs rather widely in its habits from *Photinus*, as will be seen from the following.

*Ellychnia corrusca* is most conspicuous in spring, appearing on tree trunks in New England, as early as April, and may be met with when autumn is merging into winter. Like the smaller variety *autumnalis*, it hibernates in the adult state, seeking refuge from the cold, beneath stones, in decaying logs, under tree burlapping, and beneath the looser moss about the base of tree-trunks where at times it congregates in considerable numbers. It is a decidedly hardy insect and, given the proper condition, a very large per cent. of the autumn individual seems to hibernate successfully. I confined 18 specimens (♂ and ♀) in a small brass box filled with moss and provided with a screen cover, and in late November placed it outside a window with north exposure where it remained until the middle of April. The box was brought in from time to time, slightly warmed and the beetles examined. Not all the *Ellychnia* were thus brought out of their torpor during these brief spells, but the activated beetles were very thirsty and drank eagerly from the moss which I had moistened. Of these 18 beetles exposed to temperatures that fell more than once below zero Fahrenheit, 16 were alive and healthy at the end of April. Mating takes place when the beetles are well out of hibernation. The earliest record I have in captive specimens is May 7, 1916. This pair, with other beetles, were previously given banana peel, the soft inner portions of which they consumed to some extent. As adults they are probably purely phytophagous.

The female oviposits readily in captivity. The egg is practically spherical, creamy white, and like that of *Photinus*, provided with a viscid outer membrane. It is faintly luminous for a time at least. The young larva much resembles the *Photinus* larva, though it is possibly a little broader. I was unable to rear it beyond the first moult. There are two luminous points on the eighth sternite, but these are not so pronounced as in young *Photinus* and *Photuris*, and in the same individual are sometimes fainter on one side than on the



other or they may not always be visible. I know nothing of the later larval stages or of the pupa.

The adult beetle is commonly regarded as non-luminous, and indeed this seems to hold true of the greater number of individuals. One evening while I was examining a jar containing a number of them, a single male was observed to bear a pair of faint yellowish lights, hardly to be perceived beyond an arm's length, on the eighth abdominal sternite, *i. e.*, in the very same position and segment as the larval lights. The glow was steady and sustained. This male was the only specimen which shone (or could shine) of its own accord, but by rough handling I was able to induce four other specimens to produce a very faint and evanescent glow. It seems probable that the organs are almost non-functional or vestigial and represent those of the larva. In the adult the chitin beneath, *i. e.*, ventral to the light-organs, instead of being transparent, is strongly pigmented.

#### *Lucidota atra* Fab.<sup>1</sup>

This, like the preceding species, is diurnal, and in early summer may be seen clinging to herbage or in slow flight. It is a delicate, rather broad, depressed insect, 8-11 mm. long, with the antennal joints broadly flattened. The general color is black with the lateral edges of the prothorax broadly pinkish and yellowish. I found this insect abundant at Melrose Highlands, Mass. It is luminous in all its stages, although sometimes when freshly emerged it does not glow strongly as an adult insect.

The dull whitish eggs are subspherical and hardly differ from those of *Photinus*. The larva also is rather similar, but differs in being slightly more flattened above, and in the more angulate tergites which are dilute or grayish black instead of shining black. The larva of *Lucidota* is rather more suffused with pinkish but may be most readily separated from *Photinus* in having the lateral edges of the last two abdominal tergites very broadly whitish carneous. This pattern, situated as it is on the luminous segment, permits the brilliant yellowish green light on the eighth abdominal segment to shine dorsally as well as ventrally. The light is readily controlled and may not be used for a long period even though the insect be roughly handled. Larvæ in confinement often flash out quite suddenly if dis-

<sup>1</sup> *Lucidota atra* Fab., Ent. Syst., I, 101, 1798.

turbed and this is striking when they are in some numbers. Such sudden effulgence subsides rather gradually. Only half-grown to full-sized larvæ were found. These were often taken gregariously in the fall, winter and early spring in moist earth and rubbish, decaying stumps and under stones. The pupa, in conformity with the adult insect, has the abdominal segments drawn out posteriorly, both latero-dorsally and latero-ventrally. With the exception of the dull glassy head, appendages and tip of the abdomen, it is of a delicate roseate color. It is very active at this stage. Pupæ may not shine at all times and when shining may do so with varying intensity. In one case the luminous points appeared to be on both the eighth and ninth segments but more intense on the latter. In addition, some of the pupæ when disturbed gave forth a diffuse body glow. This recalls the glow of the *Photuris* pupa. Freshly hatched adults of both sexes shone better than older specimens, though neither did so at all times. A freshly emerged female on being handled emitted a diffuse yellowish-green light, the whole abdomen and at least the clearer lateral pieces of the prothorax being involved. The light seems to be under rather slow control and suggests that the adult may be partly nocturnal. The insect hibernates in the larval stage.

#### *Pyractomena* sp.

During the afternoon of April 19, 1916, while engaged in field work for the Gypsy Moth Laboratory of the Bureau of Entomology, I took this large and somewhat remarkable lampyrid larva at Hanson, Plymouth Co., Mass., as it was ascending the trunk of a large white oak (*Quercus alba*), at a height of four or five feet. This tree, with numerous others, formed a grove in a low, rather moist area.

The length of the larva, exclusive of the head, is 22 mm. The head is very small in proportion to the size of the body, for while decidedly elongate, its very narrow and nearly cylindrical form gives it the appearance of a dark, shining rod or tube. It is furnished with a pair of sharp-pointed, sickle-like mandibles which are somewhat upcurved at their distal end. The body is rather flattened fusiform but more narrowed posteriorly. The prothorax is by far the longest of the segments, being as long as or longer than wide and drawn out and narrowed anteriorly into a sort of neck. The thoracic legs are long and slender and strongly clawed. The rather indurate

tergites have their posterior lateral angles somewhat pointed and drawn out. The pleuræ and venter are partly membranous. The last abdominal segment is provided with a highly developed pair of fleshy, retractile and multifid prolegs. The tergites are variegated wood-brown, with a dark streak bordering the paler median line. Ventrally it is more pinkish. The insect bears some resemblance to a slender larva of *Photuris* and is undoubtedly predaceous and to a degree a climbing insect. The elongate, almost minute head, which tortoise-like, can be retracted far out of sight into the prothorax, would appear well fitted for exploring crannies in the bark, etc., for prey, while the long thoracic and much divided anal prolegs facilitate its scansorial habits.

I kept the larva in a tumbler partly filled with loamy soil, which, having previously contained a lepidopterous larva, had the sides more or less spun over with silk. Towards the first of May, the *Pyractomena* had crawled up near the top of the tumbler and evidently by means of an anal secretion or a dried-up liquid of some sort had firmly suspended itself, venter towards the glass, by the tail. Its head was retracted (the pupating *Photuris* larva has the head extruded) and the two ventral lights on the eighth abdominal segment were often visible, and frequently most of the membranous portion of the body facing the glass showed a delicate effulgence. When I disturbed it the effulgence would brighten up considerably and so would the two tail lights. After having remained suspended in this quiescent stage for the matter of a week it transformed into a large pupa, the larval skin splitting laterally or ventrally and not dorsally, as with pupating Lepidoptera, and remaining shrivelled and attached to the posterior portion of the abdomen. The remarkable thing about this pupa, apart from its being suspended, is its darkly pigmented condition, which strongly suggests that it is always formed above ground and in a situation exposed to light.

The pupa is moderately stout and only slightly arcuate; the pronotum is long, and the tergites have their lateral posterior edges somewhat reflexed and pointed, making it appear rather spinous. The pronotum bears a yellowish white median line, which is bordered by a wider blackish stripe, beyond which is a wide yellowish-white edge. The remaining tergites as in the dorsum of *Photinus* larvæ are shining black and have a rather wide, dull yellowish-white median line while

ventro-lateral to the tergites there is much pink. The leg- and wing-cases are blackish. The abdomen in its softer portions is dull yellow and pink and has a brown sublateral stripe.

The comparatively long duration of the prepupal stage may partly account for the dark color of the pupa.

Judging from the single specimen I have observed this *Pyraconema* must differ rather widely in its habits from *P. lucifera* (see Wenzel, 1896) which lives in salt marsh meadows among snails.

#### *Photuris pennsylvanica* DeGeer.<sup>1</sup>

The adult beetle is elongate and rather flattened, the head is somewhat retracted under the prothorax, the antennæ eleven jointed, slender and tapering, and the eyes large. The thorax has the disc convex, with broad thin margins, and is rounded anteriorly and along the sides and subtruncate posteriorly. The legs are slender, the outer tarsal claw is bifid; the elytra are rather acute at the tip and extend well beyond the extremity of the abdomen. The general color of the head is dull yellow, with a black area on the posterior part of the vertex. The pronotum is dull yellow with the disc red and a median black stripe, while the rest of the thorax is very dark brown. The legs are paler at the base of the joints and at the apex of the femora, while the elytra are brown or piceous, with the suture, side margins, and a narrow tapering stripe on the disc, pale brownish. The abdomen is blackish brown with the posterior border of the fifth and all of the remaining sternites, yellowish. The luminous organs are yellowish and are situated on the sixth and seventh sternites. They are larger in the male. The body is clothed with fairly abundant yellowish pile, which is darker on the legs and most conspicuous dorsally. The pronotum and the elytra are densely and rather coarsely punctate. The length varies from 11 to 15 mm.

This is the largest and commonest of the brilliant New England fireflies, and from early June till the end of July, or the first week of August, both sexes may be seen along the borders of woodlands, flashing their yellowish-green light. The habitat of this species is therefore unlike that of the abundant *Photinus consanguineus*, which frequents low moist meadows. While it is true that *Photinus scintillans* flies with *Photuris* in this locality, owing largely perhaps to

<sup>1</sup> *Photuris pennsylvanica* DeGeer, Mem. Hist. des Ins., IV, 1768, 52.

the voracious appetite of *Photuris*, it does not flourish alongside its larger neighbor. Only a few *Photuris* were found in the *Photinus consanguineus* locality. As in other Lampyridæ, *Photuris* has more or less well-defined centers of distribution, areas fairly scintillating with their lights, which elsewhere are more scattered or absent. These places, where on favorable evenings the larvæ can be found in abundance, are evidently the ones in which they pass their early stages.

Both sexes of *Photuris* fly readily and rather high, but the males are more often seen on the wing than the somewhat terrestrial females. In July, the flight begins from a little before to a little after 8:00 P. M., and most of the males have settled by 9:00 P. M. While there is considerable uniformity as regards the number of flashes emitted by these insects, exceptions are common. As a rule, the males flash three or four times to a period, and the last flash is usually the least intense. Each flash is of about a second's duration, and separated from the next by considerably less. Some flash twice, another will give six very rapid flashes, but the number seems constant for each specimen. It was estimated that when in flight, the males flash for every fifteen feet traversed. They may scintillate in this manner when resting on trees or weeds. The flight of the female is more rapid and direct than that of the male, and her flashes are less intense and somewhat more variable. While on the wing she was observed emitting a dim though steady light. When alighted she flashes once or several times. In the latter case the intervals are longer than in the male.

While there seems to be little doubt that the light emissions play an important part in bringing the two sexes together, it seems equally clear that by itself, this function is less necessary in *Photuris pennsylvanica* than in the various species of *Photinus* studied by different observers. No exchange of light flashes was made out with certainty in the case of *Photuris*, and none occurred during copula. The female while shining does not necessarily assume a vertical position, as do *Photinus* and some of the European species, nor does she curve up the tip of the abdomen as in the latter. In the evening the females were usually resting in a more or less horizontal position, upon some bush or weed, or upon the ground, and the brilliant flash shone appreciably through the elytra. The photini were much less active than

the photuri, and were able to cling firmly to weeds, etc. The latter are very nimble runners and restless insects, so that the sexes should readily find one another.

When captured or roughly handled *Photuris* frequently exudes a pale honey yellow fluid from between the last coxal joints; this "blood" likewise exudes when the elytra are cut. In *Photinus*, *Ellychnia* and *Lucidota* the fluid is whitish and more viscous and flows even where the elytra may be flexed. The exudation is probably protective. The female oviposits for several nights and requires an abundance of food for her sustenance and for the development of the eggs which are in several stages of growth in her ovaries. Her appetite, to say nothing of cannibalism, is worthy of note. The male, on the other hand, seems to be a sparing eater. On several occasions a female was discovered perched upon some convenient stem, leaf, or upon the ground, devouring a male *Photinus scintillans*. One evening six females were disturbed at such meals. The fact that the victims were always males, though the females were nearly as abundant in this locality; and that the feeders were invariably females, strongly suggests that the weak *Photinus* males were drawn to their untimely ends by the lure of the greenish-yellow light of the female *Photuris*. When bottled up with *Photinus* they would readily devour the latter, despite its active exudations. When confined in the laboratory, a female would frequently overcome and devour a male of her own species, less often she would attack one of her own sex and cling tenaciously to her actively running prey. The males would not feed in captivity.

Oviposition was not observed in the field and was seen but once in the laboratory. The female thrusts her long ovipositor a few millimeters into the soil to lay the sticky, pale yellowish egg. Eggs laid in the laboratory, or better, by specimens confined in shady places out-of-doors, were deposited in the soil or among the roots of grass, either singly or in small groups. The egg, while not constant in size, averages about 0.784 by 0.677 mm. Its pale yellow color serves to distinguish it from the whitish egg of *Photinus* and *Ellychnia*. Under a hand lens it is polished, under a high magnification it has a finely dotted appearance owing to the presence of a thin membrane which contains oil-like globules and gives it the adhesive properties. When first laid the egg is soft and often more or less flat-



tened against an object, later it grows and rounds up somewhat and develops a firm and brittle shell. Long ago Newport (On the Natural History of the Glowworm, 1857) noticed the growth of the laid eggs and found them to be effulgent. Seaman (1891) says: "The eggs of the Lampyridæ and Pyrophori may be dried to their utmost without losing their photogenic property." Dubois (1898) adds that the eggs of *Pyrophorus noctiluca*, the large luminous Elaterid of the neotropical regions, shine when unfertilized, and even while in the ovarian tubes. He states that they have great affinity for moisture and will even glow when placed near a green blade of grass. Mr. H. S. Barber writes me (June, 1914) concerning *Phengodes laticollis* that "luminosity develops in the egg before hatching." The eggs of *Photuris pennsylvanica* certainly glow when deposited, and till they are from two to four days old, and therefore probably throughout their life, but the effulgence is often so faint that it can be perceived only by careful and protracted scrutiny in total darkness. In July, 1914, I squeezed several eggs out of the ovary of a living *Photuris*, and placing these in water, carefully examined them in the darkness. But they were not found to shine and so they were crushed and placed in hydrogen peroxide, when at least one egg emitted a faint luminescence.

In the laboratory eggs of *Photuris* hatched in about fifteen to eighteen days, into peculiar, very active, somewhat turtle-shaped larvæ about 2.20 mm. long. At first whitish, except for the blackish eyes and pale yellowish-brown of the feet, mouth-parts and antennæ, the larva darkens in the course of a day or two and becomes slaty gray with the head largely brownish. The length of the body is now about 2.50 mm., including the extended head 2.70 mm., its width at the third segment 1 mm. The head is depressed cylindrical, a little more than twice as long as wide and hardly one third the width of the prothorax. The eyes are simple and rather large, the antennæ short, tapering and three-jointed, the first joint is membranous and the third bears a cylindrical sense-organ distally and a lobed process before the end. The jaws are stout, arcuate and notched before the tip. The body is oblong oval, tapering more caudally, with the sides above depressed, forming a rather prominent median ridge; the prothorax is about as long as the meso- and metathorax combined, the latter two are each longer than any of the abdominal segments with the possible

exception of the ninth; the abdominal segments particularly, have the sides drawn out and curved posteriorly and armed at their apices with long strong spines; spines also occur sparingly on the dorsum, and smaller ones are scattered over the body, which is finely and irregularly granulated. The legs are slender and spinose, the tarsal claws simple though spined basally. The prolegs, of which there is but a single anal pair, have each side subdivided into six slender furcate processes and an inner shorter and stouter furcate process. All these sixteen processes are armed with rows of recurved hooks. The prolegs are less divided than in *Photinus*, and can be extended fanwise to serve both as an organ of propulsion and of adhesion, the tiny hooklets giving the insect a firm hold. The abdominal prolegs of beetle larvæ have been much studied by Brass (1914). He terms the organ, which is a development of the tenth abdominal segment, the seventh foot, and says that it finds its highest modification in the lampyrid *Luciola italica*, which has the proleg dichotomously branched into one hundred and twenty filaments. Brass suggests that it owes its development to the unsupported weight and extent of the abdomen. When fully expanded the soft fleshy foot covers a large area, and while not in use is protected by being completely withdrawn into the body cavity.

*Photuris pennsylvanica* uses its prolegs extensively in climbing weeds, and also employs them to brace itself, though often ineffectually, against the pull of its struggling prey. Occasionally it will curve the end of the abdomen over its back and use the finely divided seventh foot as a broom with which to clean its dorsum. This has also been observed in some European Lampyridæ, by Targioni Tozzetti (1865), Berlese (1909), Fabre (1913), etc. Species like *Lampyris noctiluca* that feed upon snails, thus wipe off the slime which has soiled them.

The larva of *Photuris* is capable of enduring considerable drought and of surviving for some time without food. Specimens which hatched about July 27, 1913, were offered cut-up insects, chiefly flies, which they devoured in the evening or in artificial darkness, hiding during the day in crannies and under lumps of earth. In feeding, they congregate about their food in some numbers and inserting their small extrusible heads into the victim soon convert it into a mere shell.

From August 8 to 10, approximately, most larvæ of this brood had passed into the second instar, having undergone one ecdysis. As upon hatching, they are soft and whitish for some hours, and measure about 5 mm. in total length. By August 20, many were in the third instar and 7 to 8 mm. long. The color is now quite dark, with the pale tergal markings conspicuous. The development of the brood as a whole becomes less and less uniform so that we meet with larvæ of the same age but varying considerably in size. I lost count of the instars beyond the fourth, after which there must have been three or more ecdyses. Some of my second-year larvæ moulted in the laboratory during winter. It is certain that the insect requires the greater part of two years to reach the adult stage, and it is not improbable that in some cases a longer period is necessary. The full-grown larva is from about 16 to 18 mm. long, being nearly three times as long as wide. The head is subcylindrical and about one third as wide as the prothorax; the antennæ are three-jointed, the first joint being membranous, the second partly so, and the third with a terminal and subterminal sense-organ; the mandibles are much stouter and blunter than in *Photinus*, but like the latter they are arcuate and also notched below the apex. The body is much depressed, otherwise it is fusiform, being widest a little above the middle; the prothorax is the longest segment and shaped much as in the adult; the abdominal tergites are curved posteriorly, especially the caudal ones. The legs are rather spinose. The head is largely polished black, the mouth-parts brownish, the dorsal part of the body dull brownish, sometimes quite dark, and having subdorsal yellowish-white stripes of irregular nature disposed as follows: a large one from the anterior border of the prothorax, a smaller one from its posterior edge; these are more faintly repeated on the meso- and metathorax; on the abdomen there is a pair of more or less broken inbowed stripes, becoming obsolete posteriorly, and a similar blotch near the lateral edge of each tergite. The dorsum is more or less irregularly dotted, in deep punctations, with blackish, which serves to darken the color as a whole; blackish spots are grouped inside the pale abdominal lunules, and a more or less broad arcuate line cuts into the subdorsal markings from within. On the ventral surface the color is dirty yellowish white except for some latero-ventral blotches of brown, which however are absent on sternites seven and eight and a part of nine.

The legs are pale wood brown, darker apically. The body is quite rugose, with spines along the margins and on the legs.

Throughout the summer and fall, when the days are still warm, these peculiar testudiform larvæ can be taken in goodly numbers creeping over the ground, near edges of brooks, under brushwood, and even several inches up plant stems. Most of them prove to be larvæ in the second year of their growth. Specimens in the second, third and fourth moults are less commonly seen, but all shine brightly and steadily from two little yellowish-green points on the eighth abdominal sternite. When a light is brought near them they hasten away, and when touched on the back have a habit of flattening themselves.

The feeding habits of American lampyrids are more imperfectly known than those of Europe, where Fabre, Newport and others have studied the natural history of *Lampyrus noctiluca*. As a larva, this insect feeds upon *Helix nemoralis*, *aspersa*, and probably other snails which it cautiously bites, injecting a poisonous deliquescent fluid into its prey at the same time. The mollusc is rendered inert by several of these tweaks and can then be devoured at leisure. Fabre (1913) speaks of the remarkable case of the Algerian beetle, *Drilus maroccanus*, allied to the glow-worm, which fixes itself to the surface of the snail-shell and there awaits, for days if it needs be, for the snail to open up the strong lid with which it is provided. In America, *Phenogodes* is known to feed upon myriopods, and *Pyraclomena lucifera* lives in salt marsh meadows among snails. McDermott (1910), in speaking of the larva of *Photuris pennsylvanica*, says: "These larvæ appear to be semi-aquatic in habit; at this time of the year (early September), while walking along the edge of Rock Creek, in Rock Creek Park, Washington, D. C., numerous points of greenish light, which glow slowly and then die out slowly, to glow again in a moment or so, may be seen at the very edge of the water; on investigation these proved to be the larval forms of *Photuris* clinging to moist stones, weeds, etc., and presumably preying upon the smaller living things there." On the evening of September 8, 1913, I chanced upon three *Photuris* which were disposing of a large limp earthworm they had evidently overcome a few minutes before my arrival. This is the only occasion on which I saw *Photuris* larvæ feeding in the field. In the laboratory they readily devoured cut-up insects, which they left as mere shells. Certainly snails appear to be far too scarce in

this vicinity to furnish even a little of the food. The larvæ would not touch living slugs in the laboratory, but earthworms, particularly those which had been wounded, were often attacked and eaten. A good-sized earthworm was placed in a jar with several larvæ. In the bright electric light but one was bold enough to affix itself to the hinder part of the worm, with its prothorax bent down towards its prey. It allowed the worm to pull it about, and let drag its expanded prolegs, chewing steadily and relentlessly the while. Apparently the worm suffered partial paralysis in the attacked region since it retaliated but feebly, except at the first few tweaks. In the morning the worm was found dead, with several larvæ feeding upon it. One end was quite eaten away, and here and there along its remaining length was a number of lumps which were evidently the result of bites. Another worm in the same dish remained uninjured. A decidedly large and vigorous worm, about four inches in length, was left over night in a battery jar half filled with earth and containing about thirty large larvæ. One end of the creature had been previously injured but the animal was nevertheless quite active. At 10 P. M., upon examining the jar after it had been kept in darkness for some time, it was found that the worm had been attacked and was being devoured at three different points, including the wounded end. I counted fifteen larvæ engaged at this repast. The worm was still capable of slow movement, and, if squeezed with a pair of forceps, of considerable activity. The next morning revealed a number of much distended larvæ, feeding on the remnants of their prey—two pieces, one a mere stub, the other a somewhat flaccid piece an inch and a quarter in length. It is quite probable that while earthworms form a good proportion of the food of *Photuris*, it must feed upon a diversity of other forms. The mandibles seem to be blunter and much stouter than those of most lampyrid larvæ so that the creature may devour what it can overcome. Not being provided with salivary glands, it must, like many other carnivorous beetle larvæ (Carabidæ, Dystiscidæ, etc.), inject an alimentary poison, probably secreted by the midgut, into its prey.

Unlike the more slender *Photinus*, the *Photuris* larva is hardly subterranean in its nocturnal habits and is doubtless a more extensive traveller. By the end of October, I could find but few larvæ in the field. The ones confined indoors were for the most part resting

upon the floor or suspended from the roof of well-formed cells, under a thick strip of mossy soil, but owing to the indoor warmth, none of these larvæ was in a truly resting state. The abnormal laboratory conditions were probably responsible for the development of prothetely in two individuals (see *Psyche*, XXI, p. 126, 1914). Several pupated indoors, in February and March, but the majority transformed during May. Evidently the winter larval cells are not the pupal chambers, for these were largely deserted in the spring, when the insects took some food. On March 31, 1915, I found a few second-year *Photuris* larvæ hibernating under small stones, in earthen chambers. Situated as they are, from one to several inches below the surface of the ground, they successfully pass through the rigorous winters of New England.

A pupating larva rests quietly on its back, with the head quite extruded by the developing pupal head; the skin finally splits along the mid-dorsum and the pupa is disclosed. Pupating larvæ have a diffuse glow. But one pupa was found in the field, and the moist soil which I had slightly disturbed with my foot revealed this decidedly effulgent specimen. The pupa has an extended length of 11 mm. and an arcuate length of 9 mm. It is robust and somewhat less arcuate than *Photinus* pupæ, and has the hind legs free for a considerable distance. The head and appendages are translucent whitish, the abdomen is more opaque and with a slight creamy yellow tinge dorsally. This tinge extends up to and includes the metathorax, the yellow being divided by the line of the dorsal vessel. The insect is nowhere pinkish. The thin free edges of the first abdominal segments are somewhat drawn out laterally and dorsally and bear a loose tuft of brown hair; more such hair occurs at the end of the abdomen and especially along the edges of the prothorax and more sparsely along the posterior border of the abdominal segments. The pupa retains the two steady and strongly luminous points of the larvæ on the eighth abdominal segment, and, in addition, the head and the thorax are effulgent, so that it can be seen in the darkness for a distance of a dozen feet or more. At times the abdomen is faintly luminous, and when near emergence the adult light-organs also function. The pupal period is quite brief. The pupa is rather active, wriggling decidedly. The larval lights as well as the diffuse glow of the head and thorax disappear when the adult hatches, or shortly thereafter. I ob-



served an adult female bred in the laboratory, and probably a day old, which on being brought into darkness, was found to have the adult as well as the larval light-organs shining steadily, and in addition, the vertex and frons of the head (where the chitin was transparent) shone also. The dorsum of the thorax down to the abdomen, in the more transparent portions, had an unmistakable glow. Such conditions however were not found in the field, nor upon dissecting older specimens. It is evident that a considerable time must elapse after it has hatched from the pupa before the insect is really firm and mature, when the photogenic granules are seen to glow only in the luminous organs of the adult.

But little was done on the internal anatomy of this insect. The larval digestive and nervous systems are practically the same as in *Lampyris noctiluca*, as figured by Vogel (1915). If we compare the nervous system of the larva and adult *Photuris*, the following points will be noted: the larva has a total of thirteen distinct ganglia in the nervous system, the adult twelve; in the former the brain is in the cervical region, behind the head, and the last two abdominal ganglia, the seventh and eighth, the latter being compound, are separated by a distinct though comparatively short pair of connectives; in the adult the brain, of course, lies within the head and is more closely connected with the subœsophageal ganglion, the first abdominal is very near to, though distinct from the third thoracic ganglion and the seventh and eighth are fused into one oblong ganglion with a median constriction. Thus it is seen that there is no considerable difference between these generalized systems in the larva and adult.

#### RESUMÉ.

1. Biological studies were made on six different species of fireflies in New England, viz., *Photinus consanguineus*, and *scintillans*, *Ellychnia corrusca*, *Lucidota atra*, *Pyratomena* sp. and *Photuris pennsylvanica*.

2. Of these, *Photuris pennsylvanica* is the most brilliant and *Ellychnia corrusca* the faintest in luminescence in the adult stage.

3. In the case of *Photuris* and *Photinus* at least, the larval light organ is different from that of the adult one which replaces it at maturity.

4. The light organ of the adult is probably used chiefly for the

bringing together of the male and female, is more brilliant in one than in the other sex and is readily controlled.

5. The adult female of *Photuris* is carnivorous and very voracious and even cannibalistic. The other genera seem to be herbivorous as adults.

6. Ova were obtained from all but *Pyractomena*. They are sub-spherical and at first sticky and less than 1 mm. long. They are deposited a short distance in soil, moss, etc. That of *Photuris* has a yellowish tinge, the remaining five are dull whitish. All are for a time at least faintly luminous.

7. The larvæ of *Photinus*, *Ellychnia* and *Lucidota* are elongate and somewhat depressed and more or less pinkish ventrally—those of *Pyractomena* and *Photuris* are wider, flattened fusiform, and the latter is nowhere pink: The larvæ of *Photinus* and *Lucidota* are very largely subterranean, but *Pyractomena* is probably in part arboreal while the largely terrestrial *Photuris* frequently ascends weeds.

8. The larvæ are probably all carnivorous and *Photuris* devours earthworms with avidity.

9. The larvæ are all luminous—two points on the eighth abdominal sternite furnish the rather slowly controlled luminescence.

10. The larval life, perhaps with the exception of *Ellychnia corrusca*, extends in most cases over the greater part of two years.

11. *Ellychnia corrusca* hibernates as an adult beneath moss, logs, etc., the rest hibernate as larvæ.

12. The pupæ are luminous. The pupa of *Pyractomena* is pigmented and suspended like that of a Coccinellid, the others are pallid and formed beneath the ground. This stage is brief.

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